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# FOOD HABITS AND FORAGING ECOLOGY OF AMERICAN KESTRELS IN THE SEMIARID FORESTS OF CENTRAL ARGENTINA

José Hernán Sarasola[1], Miguel Angel Santillán and Maximiliano Adrián Galmes
*Centro para el Estudio y Conservación de las Aves Rapaces en la Argentina, Avda. Uruguay 151, FCEyN—Universidad Nacional de La Pampa, 6300 Santa Rosa, La Pampa, Argentina*

Abstract.—The annual diet of the American Kestrel (*Falco sparverius*) was studied by analyzing 705 pellets and prey remains collected in a semiarid forest area of central Argentina. The diet composition fluctuated seasonally but was composed primarily of invertebrates, followed by small mammals, birds, and reptiles. Based on biomass, vertebrate prey was the major component of the diet in winter and spring. We found significant numerical differences between prey consumed by adult and nestling kestrels. Percentages of small mammal prey were higher in the diet of adults than in the nestlings, but rodents consumed by nestlings were larger in size than consumed by adults. Nestlings also ate more birds and reptiles than adults. Based in biomass contribution of vertebrate and invertebrate prey to the diet during non-breeding and breeding seasons, American Kestrels in semiarid forest of Central Argentina were more carnivorous than insectivorous predators. Differences between adult and nestling diets emphasized the importance of collecting samples from perches and nests when kestrel food habits are being studied during the breeding season.

Key Words: *American Kestrel;* Falco sparverius; *food habits; breeding season; semiarid forest; Central Argentina.*

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HABITOS DE ALIMENTACIÓN Y ECOLOGIA DE FORRAJEO DE CERNÍCALOS AMERICANOS EN LOS BOSQUES SEMIARIDOS DEL CENTRO DE ARGENTINA

Resumen.—Estudiamos la composición anual de la dieta del Cernícalo Americano (*Falco sparverius*) en un área de bosque semiárido del centro de Argentina a través del análisis de 705 egagrópilas y restos presas. La composición de la dieta fluctuó estacionalmente pero fue compuesta en primer orden por invertebrados, seguidos en importancia por mamíferos, aves y reptiles. En términos de biomasa, los vertebrados fueron predominantes en la dieta en invierno y primavera. Encontramos diferencias significativas entre las presas consumidas por los cernícalos adultos y sus pollos. Los porcentajes de ocurrencia de pequeños mamíferos fueron mayores en la dieta de los adultos, pero los roedores consumidos por los pollos fueron más grandes. Además los pollos consumieron un mayor número de aves y de reptiles que los adultos. Tomando como base el aporte en biomasa de vertebrados e invertebrados durante las estaciones reproductivas y no-reproductivas, el Cernícalo Americano se presenta como un predador carnívoro en lugar de insectívoro para los bosques semiáridos del Centro de Argentina. Las diferencias observadas entre las dietas de los adultos y los pollos demuestran la importancia de conducir muestreos tanto en perchas como en nidos cuando se estudia el hábito alimenticio de este cernícalo durante la estación reproductiva.

[Traducción de los autores]

The American Kestrel (*Falco sparverius*) is widely distributed in North, Central, and South America inhabiting many different habitats and landscapes (Brown and Amadon 1968). In Argentina, the kestrel occupies subtropical forests in the north through shrubland steppes in Patagonia (Narosky and Yzurieta 1989, De la Peña and Rumboll 1998). The ecology and behavior of kestrels have been studied extensively (e.g., Roest 1957, Balgooyen 1976, Koplin et al. 1980, Rudolph 1982, Smallwood 1987, Varland et al. 1993). The food habits of this species have been documented in various habitats, but most of these studies have been carried out in Central and North America (see Heintzelman 1964 for a review, Jenkins 1970, Balgooyen 1976, Cruz 1976, Collopy and Koplin 1983). In the southernmost extreme of its range, the diet of kestrels has

[1] Present address: Department of Applied Biology, Estación Biológica de Doñana (CSIC), Avda. María Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain; e-mail address: sarasola@ebd.csic.es

been examined only in Chile (Greer and Bullock 1966, Yañez et al. 1980, Simonetti et al. 1982) and there is one anecdotal record on the stomach contents from northeast Argentina (Beltzer 1990). All of these studies have quantified the diets, but no attempt has been made to assess the diet based on prey biomass. In addition, research has focused on the diet either during the winter or the breeding season, and no systematic study of the annual variation diet within a particular habitat has been completed. Similarly, studies in diet of kestrels during the breeding season have employed several different approaches (Lamore 1963, Balgooyen 1976), but none include a comparative analysis between prey consumed by adults and nestlings.

Here, we report the food habits of the American Kestrel in the semiarid forest of central Argentina and analyze the numerical and biomass contributions of vertebrate and invertebrate prey to the diet. We examine seasonal variations in the diet and show the differences in prey consumed by adults and nestlings during the breeding season.

## STUDY AREA

This study was conducted in Parque Luro Reserve (36°55′S, 64°16′W), located in La Pampa province of central Argentina. The reserve (7604 ha) consists mainly of xerophytic open forests of caldén (*Prosopis caldenia*) which represents the characteristic landscape of the Espinal biome in the semiarid pampas of Argentina (Cabrera 1976). Forest areas in the reserve differ structurally, in part because of soil features, but mostly because of the effects of human disturbance. *Stipa* spp. are the dominant herbaceous species, and *Condalia microphylla, Lycium chilense, L. gillesianum,* and *Schinus fasciculatus* are the common shrub species when a middle stratum is present. Fieldwork was conducted in the tourist area of the reserve (450 ha) where forest fragmentation has been greater due to the clearing of native vegetation for the development of tourist and recreation facilities. Broad, open areas of natural *Stipa* grassland are common in this part of the reserve. Habitats surrounding the reserve consist of agricultural areas planted with crops, and perennial and annual pastures. Historically, these semiarid forests have been characterized as having hot summers and cold winters with low humidity and low annual rainfall, typically concentrated in spring and summer. However, unusually excessive rains have occurred during the last 11 years and the mean annual precipitation has increased to 791 ± 336 mm ($N = 11$).

## METHODS

We collected American Kestrel pellets monthly from March 2000 to February 2001. Pellets and prey remains were collected beneath kestrel perches throughout the year and from five nest boxes occupied by pairs of kestrels during the breeding season. Pellets from adult kestrels were collected in perches located in three of the five territories where nest boxes were occupied. Pellets and prey remains found in nest boxes were assumed to represent the diet of nestlings and collected during the post-hatching period until the time when young kestrels left. Only fresh and compact pellets were collected both from perches and nest boxes.

Pellets collected were hydrated and broken apart by hand and remains of prey items were separated for identification. Mammals and lizards were identified on the basis of skulls and dentaries using reference collections and keys (Pearson [1995] for mammals and Cei [1986] for lizards) to the species and subfamily levels, respectively. Arthropods were identified using mandibles, heads, elytra, and any other parts that allowed identification to the subfamily level. In order to estimate the minimum number of individual prey in each sample, skulls were counted for mammal prey; skulls, legs, and feet were used for birds; skulls and tails were used for lizards; and whole heads, feet, elytra and mandibles were used for insects. When only hairs, bones, feathers, or scales were found in a pellet, one individual prey was counted in the sample and classified as unidentified.

To compute prey biomass, we obtained the mean body mass of adult small mammal species from Tiranti (1992) and Tiranti (unpubl. data) provided data for the body mass of juvenile tuco tucos (*Ctenomys* spp.). The mean body mass of the bird species was obtained from Fiora (1933). Unidentified passerine body mass was calculated as the arithmetic mean of the known species that we recorded in the diet (Fiora 1933, Salvador 1988, 1990). Lizard and arthropod biomass were obtained from specimens collected in the study area in three pit-fall traps (Corn 1994). Mean weights were calculated from six lizards (*Teius* spp. and *Cnemidophorus* spp.), 56 orthopterans, seven mantids (Mantidae), 46 ants (Formicidae), 18 homopterans, 37 coleopterans, 21 spiders (Araneae) and 15 scorpions (Bothruridae). For unidentified mammals, reptiles, and birds, we assigned them the average mass of prey contained in each taxa for the same sample.

We used chi-square analysis (Zar 1996) to test differences in diet between seasons and between the diets of adults and nestling kestrels during the breeding season. For this analysis, prey taxa were grouped into four major classes (vertebrates, Orthopterans, Coleopterans, and others) and their frequencies were pooled by season (21 March–21 June = Autumn, 21 June–21 September = Winter, 21 September–21 December = Spring, and 21 December–21 March = Summer). Correlation analysis was used to examine the relationship among percentage of Coleopterans and Orthopterans in the diet. These percentages were subjected to an angular transformation prior to analysis (Zar 1996).

Levin's index of food niche breadth (Marti 1988) was calculated for each sample as follows: $B = 1/\Sigma_{i=1}^{n} p_i^2$, where $p_i$ is the proportion of prey in different categories To compare diet breadth between samples with different numbers of prey categories, we calculated the standardized food niche breadth following Colwell and Futuyma (1971): $B_{sta} = (B_{obs} - B_{min})/(B_{max} - B_{min})$, where $B_{min}$ is the minimum niche breadth possible ($N = 1$), $B_{obs}$ = number of prey types observed, and $B_{max} = N$. This index ranged from 0–1. In order to evaluate differences in size of prey consumed by adult and young American Kestrels, we calculated the mean prey size by summing the products of the number of individual prey items and their mass and then dividing by the total number of prey in the sample. Our statistical test comparing this parameter was based on the assumption that prey sizes consumed were normally distributed.

Comparative studies have demonstrated that pellet analysis is subject to a number of biases for specific raptor species (e.g., Mersmann et al. 1992). Although no similar studies have been conducted to assess these biases in the analysis of the diet of the American Kestrel, our results must be considered potentially biased in representing some prey types in the diet.

## RESULTS

During the study period, we collected 284 pellets and 421 prey remains. A total of 3127 prey items were identified from three vertebrate and six invertebrate classes. Arthropods comprised about 93% of the total prey items followed by rodents (6%), birds (1%), and reptiles (<1%). In terms of biomass, rodents accounted for 47% of the diet followed by insects (42%), birds (8%), and reptiles (3%).

**Seasonal Diet Composition.** We found significant differences in the diet of American Kestrels between seasons ($\chi^2 = 256$, df = 9, $P < 0.01$). Orthopterans, mainly grasshoppers, were the most common prey item in all the seasons, but their occurrence in the diet varied seasonally (Table 1). The percentage of Orthopterans in diet was negatively, but non-significantly, correlated with the percentage of Coleopterans ($r = -0.90$, $N = 4$, $P = 0.09$; Fig. 1), which were only important in winter and spring when the percentage of Orthopterans decreased in the diet. The greatest food niche breadth and mean prey size were recorded during the breeding season due to the frequent occurrence of mammals, birds, and reptiles in the diet. The biomass of vertebrate prey was higher than for invertebrates in winter (64.4%) and spring (68.6%; Fig. 2), but the biomass of Orthopteran prey was higher (70.9%) in summer than all other prey groups combined.

**Diets of Adult and Nestling Kestrels.** On a numerical basis, we found significant differences between the diets of nestling and adult kestrels during the breeding season ($\chi^2 = 85.2$, df = 3, $P < 0.01$) (Table 2). The standardized food niche breadth of nestling was greater than that of adults, but the mean prey size was approximately the same for both age groups (Table 2). Although similar percentages of invertebrates were found in both diets, nestlings consumed more birds and reptiles than their parents, while adults ate comparatively more rodents than nestlings. In addition, a partitioned analysis of the standardized food niche breadth resulted in similar values for adults and nestlings for invertebrate prey (adult breadth = 0.20 vs. nestling breadth = 0.21), but a greater index for nestlings when we considered only vertebrate prey (adult breadth = 0.22 vs. nestling breadth = 0.39). Considering the mean size of vertebrate prey, prey consumed by nestlings were also larger than prey consumed by adults (36.1 g and 26.8 g, respectively).

## DISCUSSION

We found American Kestrels in semiarid forests of central Argentina to be generalized predators of invertebrate and small vertebrate animals. Insects occurred in the diet throughout the year with decreasing percentages of one insect prey offset by the increased ingestion of another insect group, making the total percentage of arthropods almost constant over the seasons. Based on our observations of insects and small vertebrates in the study area, we suggest that these fluctuations in invertebrate prey consumed were due to seasonal changes in their availability rather than due to prey selection by the kestrels. From 2225 orthopterans and coleopterans collected seasonally throughout the study period, only 6% of them were recorded during winter while 47% of the total were collected in summer.

The kestrels preyed most heavily on large prey such as vertebrates, only in winter when the prey were breeding. As far as rodents, adults preyed most heavily on tuco tucos (juvenile body mass = 80 g) which they delivered to their young, and on vesper mice (*Calomys* spp.; body mass = 16 g), which they ate themselves. Even though all of the tuco tucos consumed were juveniles, they were considerably heavier when compared to the kestrel's body mass and with the body masses of available alternative mammalian prey. Similar prey sizes have been reported by Lamore (1963) and Balgooyen (1976), both of whom analyzed the diets of kestrels during the breeding season. Selection of different-sized rodent prey during the breeding season may be due to the different energy requirements of adult and nestling kestrels. Balgooyen (1976) found that a brood of four nestling kestrels needed almost twice the prey mass required by their parents between hatching and post-fledging (3973 g for four nestlings vs. 2142 g for the pair of

Table 1. Seasonal composition of the diet of American Kestrels (*Falco sparverius*) in semiarid forest in Parque Luro Reserve, central Argentina. *N* = Number of Prey and % = Percent Frequency.

| | MASS (g) | AUTUMN | | WINTER | | SPRING | | SUMMER | |
|---|---|---|---|---|---|---|---|---|---|
| | | *N* | % | *N* | % | *N* | % | *N* | % |
| Vertebrates | | | | | | | | | |
| Rodents (subtotal) | | 32 | 4.7 | 75 | 7.8 | 67 | 6.3 | 6 | 1.4 |
| *Calomys* spp. | 16 | 10 | 1.5 | 14 | 1.5 | 21 | 2.0 | 1 | 0.2 |
| *Oligoryzomys flavescens* | 22 | 2 | 0.3 | 8 | 0.8 | 4 | 0.4 | — | — |
| *Akodon molinae* | 38 | — | — | 6 | 0.6 | 1 | 0.1 | — | — |
| *Akodon azarae* | 22 | 3 | 0.4 | 5 | 0.5 | 6 | 0.6 | — | — |
| *Graomys griseoflavus* | 61 | — | — | — | — | 1 | 0.1 | — | — |
| *Reithrodon auritus* | 74 | — | — | — | — | — | — | 1 | 0.2 |
| *Eligmodontia typus* | 17 | — | — | 1 | 0.1 | 1 | 0.1 | — | — |
| *Ctenomys* spp. | 80 | — | — | — | — | 5 | 0.5 | — | — |
| Rodents unidentified | | 17 | 2.5 | 41 | 4.3 | 28 | 2.6 | 4 | 1.0 |
| Reptiles (subtotal) | | 1 | 0.1 | — | — | 11 | 1.0 | — | — |
| Polychrotidae | 32 | — | — | — | — | 1 | 0.1 | — | — |
| Teidae | 29 | — | — | — | — | 10 | 0.9 | — | — |
| Reptiles unidentified | | 1 | 0.1 | — | — | — | — | — | — |
| Birds (subtotal) | | 1 | 0.1 | 1 | 0.1 | 27 | 2.5 | — | — |
| Passeriformes | 28 | — | — | 1 | 0.1 | 23 | 2.2 | — | — |
| *Columbina picui* | 47 | — | — | — | — | 3 | 0.3 | — | — |
| Bird unidentified | | 1 | 0.1 | — | — | 1 | 0.1 | — | — |
| Invertebrates | | | | | | | | | |
| Orthoptera (subtotal) | | 516 | 75.8 | 438 | 45.5 | 617 | 57.8 | 338 | 81.1 |
| Acrididae | 2.5 | 491 | 72.1 | 374 | 38.9 | 342 | 32.1 | 303 | 72.7 |
| Tettigoniidae | 2 | 14 | 2.1 | 8 | 0.8 | 25 | 2.3 | 11 | 2.6 |
| Gryllidae | 1.2 | 11 | 1.6 | 56 | 5.8 | 250 | 23.4 | 24 | 5.8 |
| Mantodea | | | | | | | | | |
| Mantidae | 1.4 | 33 | 4.8 | 8 | 0.8 | 11 | 1.0 | 26 | 6.2 |
| Hymenoptera | | | | | | | | | |
| Formicidae | 0.1 | 55 | 8.1 | 301 | 31.3 | 157 | 14.7 | 10 | 2.4 |
| Homoptera | | | | | | | | | |
| Cicadidae | 1.3 | 2 | 0.3 | — | — | 70 | 6.6 | 8 | 1.9 |
| Coleoptera (subtotal) | | 37 | 5.4 | 133 | 13.8 | 89 | 8.3 | 27 | 6.5 |
| Scarabaeidae | 1.1 | 26 | 3.8 | 44 | 4.6 | 64 | 6.0 | 19 | 4.6 |
| Carabidae | 1.3 | 11 | 1.6 | 89 | 9.3 | 24 | 2.2 | 6 | 1.4 |
| Curculionidae | 1 | — | — | — | — | — | — | 1 | 0.2 |
| Cerambycidae | 1 | — | — | — | — | — | — | 1 | 0.2 |
| Tenebrionidae | 1 | — | — | — | — | 1 | 0.1 | — | — |
| Arachnids | | | | | | | | | |
| Scorpionida | 8 | 4 | 0.6 | 6 | 0.6 | 5 | 0.5 | 2 | 0.5 |
| Araneae | 1 | — | — | — | — | 13 | 1.2 | — | — |
| Total number of prey items | | 681 | | 962 | | 1067 | | 417 | |
| Food niche breadth | | 1.79 | | 3.48 | | 5.00 | | 1.82 | |
| Standardized food niche breadth | | 0.07 | | 0.19 | | 0.20 | | 0.07 | |
| Mean prey size (g) | | 3.47 | | 3.71 | | 4.43 | | 2.74 | |

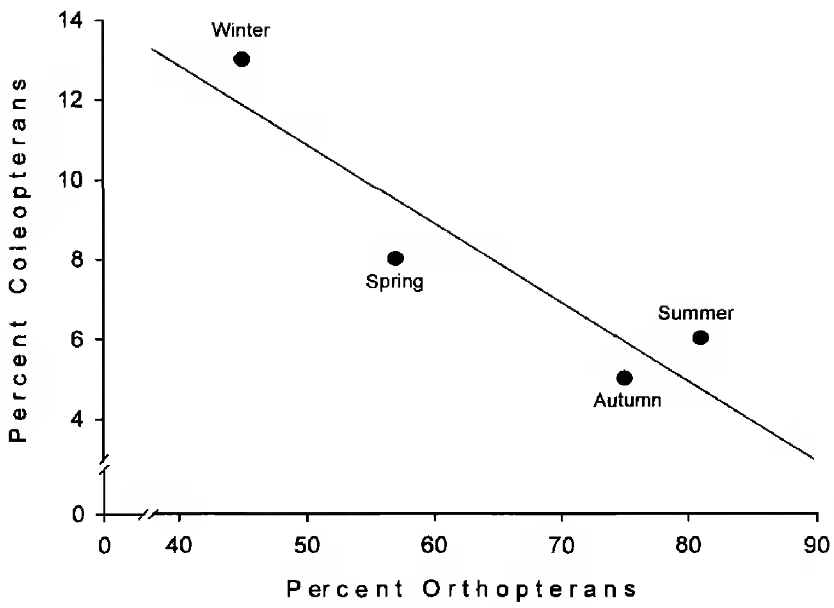


Figure 1. Relationship between percentage of Orthopterans versus percentage of Coleopterans in the diet of American Kestrels (each data point represents a season). The regression line is drawn only to emphasize the trend observed.

adults). High-energy demands of the nestlings might also explain why adults ate few birds, but fed a large number of birds to their nestlings. Birds such as House Sparrows (*Passer domesticus*) have been shown to have higher fat and gross energy content than voles (*Microtus pennsylvanicus*), and grasshoppers (*Melanoplus femur rubrum*) (Bird et al. 1982).

The kestrels we studied appeared to be rather opportunistic in their feeding behavior when we consider the occurrence of tuco tucos in their diet. This fossorial, medium-sized rodent spends most of its life underground living in long and complex burrow systems feeding on roots and grasses (Redford and Eisenberg 1992). Kestrels probably prey on the young tuco tucos when they disperse from parental burrows.

Quantitative analyses of prey have shown the insectivorous nature of kestrels. However, an inverse relationship occurs when invertebrate and vertebrate biomasses in the diet are considered throughout the seasons. Jaksic et al. (1981) and Jaksic and Delibes (1987) have classified kestrels as carnivorous/insectivorous (in that order) and within the insect feeding guild, while Jaksic et al. (1993) classified kestrels as an omnivorous predator on the basis of dietary data collected during the breeding and nonbreeding (wintering) sampling periods. In all these studies, kestrels were trophically closer to Burrowing Owls (*Speotyto cunicularia*), which Silva et al. (1995) have suggested belong to a carnivorous instead of an insectivorous guild, based on the biomass dominance of vertebrate prey in the breeding and nonbreeding seasons (see Bellocq 1988). Vertebrate prey reflected the same prevalence in the kestrel diet in our study. When we combined our data into nonbreeding (autumm and winter) and breeding (spring

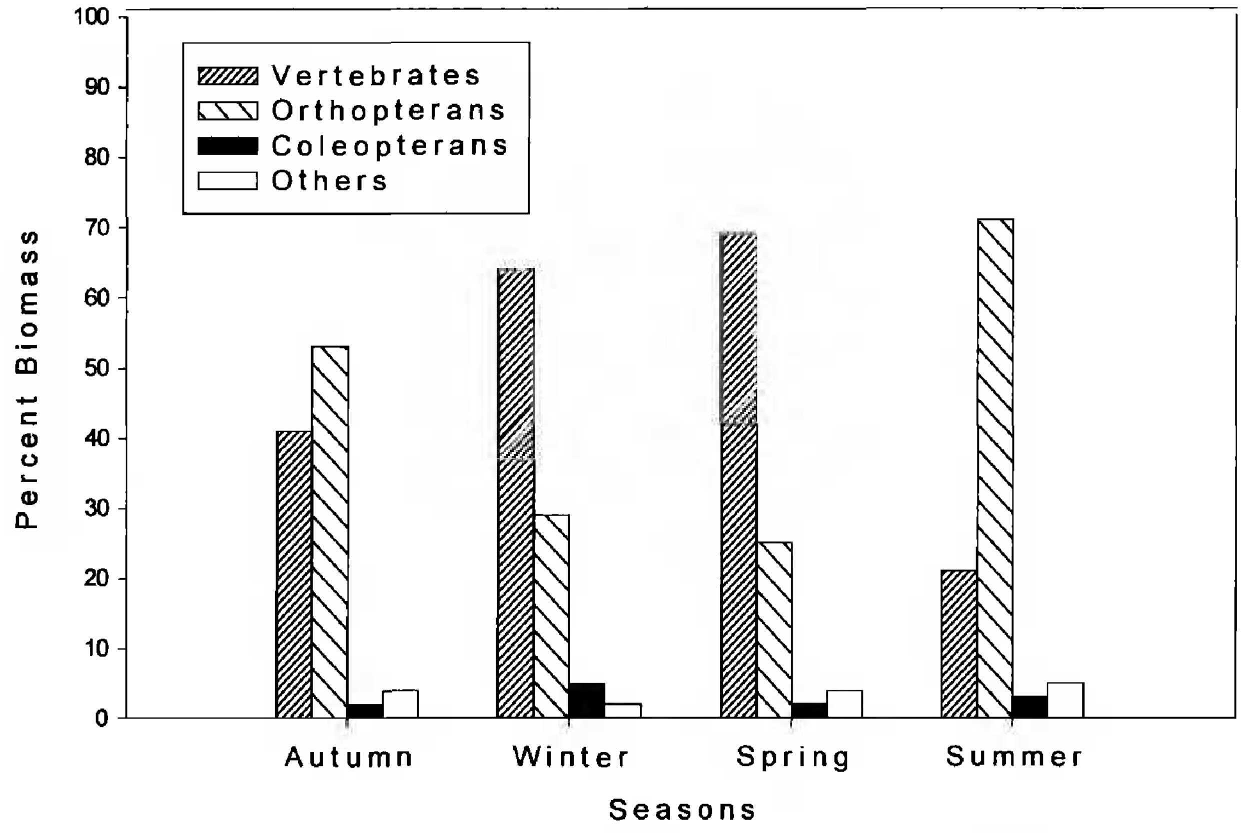


Figure 2. Percentage of biomass by season of the four major groups (Vertebrates, Orthopterans, Coleopterans, and other) of prey in the diet of American Kestrels in Parque Luro Reserve, Argentina.

Table 2. Composition of the diets of adult vs. nestling American Kestrels during breeding in Parque Luro Reserve Data from breeding season 2000 is pooled by age class ($N$ = Number of Prey).

| | ADULTS | | | NESTLINGS | | |
|---|---|---|---|---|---|---|
| | *N* | PERCENT FREQUENCY | PERCENT BIOMASS | *N* | PERCENT FREQUENCY | PERCENT BIOMASS |
| Vertebrates | | | | | | |
| Rodents (subtotal) | 56 | 10.1 | 62.2 | 11 | 2.2 | 26.5 |
| *Calomys* spp. | 21 | 3.8 | 14.1 | — | — | — |
| *Oligoryzomys flavescens* | 4 | 0.7 | 3.7 | — | — | — |
| *Akodon molinae* | 1 | 0.2 | 1.6 | — | — | — |
| *Akodon azarae* | 6 | 1.1 | 5.5 | — | — | — |
| *Graomys griseoflavus* | 1 | 0.2 | 2.6 | — | — | — |
| *Eligmodontia typus* | 1 | 0.2 | 0.7 | — | — | — |
| *Ctenomys* spp. | — | — | — | 5 | 1.0 | 17.1 |
| Unidentified rodents | 22 | 4.0 | 34.1 | 6 | 1.2 | 9.5 |
| Reptiles (subtotal) | 1 | 0.2 | 1.2 | 10 | 2.0 | 12.5 |
| Polychrotidae | — | — | — | 1 | 0.2 | 1.4 |
| Teidae | 1 | 0.2 | 1.2 | 9 | 1.8 | 11.1 |
| Birds (subtotal) | 3 | 0.5 | 4.7 | 24 | 4.7 | 30.3 |
| Passeriformes | 1 | 0.2 | 1.2 | 22 | 4.3 | 26.3 |
| *Columbina picui* | 1 | 0.2 | 2.0 | 2 | 0.4 | 4.0 |
| Unidentified birds | 1 | 0.2 | 1.6 | — | — | — |
| Invertebrates | | | | | | |
| Orthoptera (subtotal) | 254 | 45.7 | 25.8 | 363 | 71.0 | 25.0 |
| Acrididae | 234 | 42.1 | 24.5 | 108 | 21.1 | 11.5 |
| Tettigoniidae | 11 | 2.0 | 0.9 | 14 | 2.7 | 1.2 |
| Gryllidae | 9 | 1.6 | 0.5 | 241 | 47.2 | 12.3 |
| Mantodea | | | | | | |
| Mantidae | 5 | 0.9 | 0.3 | 6 | 1.2 | 0.4 |
| Hymenoptera | | | | | | |
| Formicidae | 153 | 27.5 | 0.6 | 4 | 0.8 | — |
| Homoptera | | | | | | |
| Cicadidae | 1 | 0.2 | 0.1 | 69 | 13.5 | 3.8 |
| Coleoptera (subtotal) | 75 | 13.5 | 3.6 | 14 | 2.7 | 0.8 |
| Scarabaeidae | 61 | 11.0 | 2.8 | 3 | 0.6 | 0.1 |
| Carabidae | 13 | 2.3 | 0.7 | 11 | 2.2 | 0.6 |
| Tenebrionidae | 1 | 0.2 | 0.0 | — | — | — |
| Arachnids | | | | | | |
| Scorpionida | 4 | 0.7 | 1.3 | 1 | 0.2 | 0.3 |
| Araneae | 4 | 0.7 | 0.2 | 9 | 1.8 | 0.4 |
| Total number of prey items | | 556 | | | 511 | |
| Food niche breadth | | 3.44 | | | 3.38 | |
| Standardized food niche breadth | | 0.13 | | | 0.17 | |
| Mean prey size (g) | | 4.30 | | | 4.59 | |

and summer) seasons, the percentage of vertebrate biomass was higher than invertebrates during the nonbreeding season (54%), but also during the breeding season (55%). Therefore, we agree with Jaksic et al. (1981) and Jaksic and Delibes (1987) and consider the kestrel to be a carnivorous/insectivorous predator.

Finally, demonstration of significant differences between the diets of adult and nestling kestrels indicated that food habit studies of this raptor should take into account age-related differences in the diet. If the diet during the breeding season is to be described, samples of pellets and prey remains should be collected both at the nest site and from perches used by the adult kestrels.

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